The Journal of Wildlife Management 83(8):1773–1786; 2019; DOI: 10.1002/jwmg.21749

Research Article

Greater Sage-Grouse Habitat Function Relative to 230-kV Transmission Lines

CHAD W. LEBEAU,[1] *Western EcoSystems Technology, Inc., 1610 Reynolds Street, Laramie, WY 82072, USA*
KURT T. SMITH, *Western EcoSystems Technology, Inc., 1610 Reynolds Street, Laramie, WY 82072, USA*
MATTHEW J. HOLLORAN, *Operational Conservation LLC, 2636 Cherry St., Fort Collins, CO 80521, USA*
JEFFREY L. BECK, *University of Wyoming, Department of Ecosystem Science and Management, Dept 3354, 1000 East University Avenue, Laramie, WY 82071, USA*
MANDY E. KAUFFMAN, *Western EcoSystems Technology, Inc., 1610 Reynolds Street, Laramie, WY 82072, USA*
GREGORY D. JOHNSON, *Western EcoSystems Technology, Inc., 1610 Reynolds Street, Laramie, WY 82072, USA*

ABSTRACT Greater sage-grouse (*Centrocercus urophasianus*) is a landscape-level species that requires large tracts of intact sagebrush (*Artemisia* spp.). Loss of functional habitat resulting from increased demand for energy generation, transmission, and distribution within greater sage-grouse habitats in the western United States has the potential to negatively affect this species. We monitored 346 radio-marked female greater sage-grouse from 2009 to 2014 to evaluate the potential effects of 27-m-tall, 230-kilovolt (kV) wood-pole, H-frame transmission lines on greater sage-grouse habitat selection and demography. We modeled the effect of the transmission lines in 2 different study areas simultaneously using consistent habitat data. Previous research in our study areas suggested that the effect of transmission lines was potentially confounded by other habitat features. We accounted for these potential confounding effects by estimating habitat suitability before estimating the effect of transmission lines. We combined habitat selection and demography results to estimate habitat function relative to transmission lines and inform management recommendations. Overall, we found evidence that transmission lines had a negative effect on greater sage-grouse habitat selection and survival within our study areas over 6 years, but the magnitude of this effect varied by habitat suitability and proximity to occupied leks. The effect of transmission lines on habitat function extended 1.0 km from a transmission line in habitats within 3.1 km of an occupied lek compared to 0.50 km from a transmission line in habitats beyond 3.1 km from occupied leks. Based on these results, we suggest future power line placement relative to sage-grouse nesting, brood-rearing, and summer habitats consider potential effects to sage-grouse habitat selection and demography. Effects can be minimized by incorporating design features that discourage avian predator perching and siting power lines in habitats with lower suitability and, in our study area, habitats beyond 3.1 km from occupied leks. © 2019 The Wildlife Society.

KEY WORDS *Centrocercus urophasianus*, energy development, fitness, power lines, survival, transmission.

Public demand for electricity has increased as a result of the expanding human population and industrial activities, resulting in >1.1 million km of high-voltage transmission lines in the United States (Giles and Brown 2015). The extent of power lines (transmission and distribution lines) is expected to increase with continued energy supply demands. Greater sage-grouse (*Centrocercus urophasianus*; i.e., sage-grouse), a species of conservation concern across the western United States (80 Federal Register 59857), is a landscape-level species that requires large tracts of intact sagebrush (*Artemisia* spp.) communities. The increase in demand for energy generation, transmission, and distribution within sage-grouse habitats has the potential to affect this species similar to other anthropogenic features (Naugle et al. 2011).

Power lines have the potential to directly and indirectly negatively affect sage-grouse populations. Direct mortality caused by colliding with power lines has been documented (Beck et al. 2006); however, indirect effects on population parameters are not well understood because of the lack of well-designed studies and various power line designs. Most power lines were established prior to large-scale sage-grouse studies, which makes it difficult to estimate the extent and magnitude of indirect effects of power lines on current populations (Johnson et al. 2011). In addition, a lack of newly established power lines limits our ability to implement well-designed studies to address potential indirect effects with pre-development data. Based on the few studies that exist, however, the extent and magnitude of effects appear to vary based on power line characteristics, amount

Received: 30 November 2017; Accepted: 15 July 2019

---

[1] *E-mail: cwlebeau@west-inc.com*

of available habitat, and the affected population parameter (Armentrout and Hall 2005, Schroeder 2010, Westover et al. 2016, Gibson et al. 2018, Kohl et al. 2019).

The variability among studies and power lines (e.g., voltage, size, configuration) makes it difficult to understand the potential effects of power lines on sage-grouse populations. This variability could be due to study design, study location, and other factors, such as landscape configuration and habitat characteristics that potentially confound inference (Walters et al. 2014, Westover et al. 2016, Kohl et al. 2019). For example, power lines are a linear feature often co-located with other linear anthropogenic features, such as roads, making it difficult to disentangle which feature is potentially affecting a sage-grouse population. In addition, interactive relationships between biotic, abiotic, and anthropogenic factors suggests that pulses in sage-grouse population growth, such as high recruitment in response to increased precipitation, may be mediated by habitats available to a population (Blomberg et al. 2012, Kohl et al. 2019). The extent and magnitude of these interactive effects may be difficult to assess because of potential confounding issues and inherent characteristics of the affected sage-grouse population.

There is some evidence that power lines negatively affect sage-grouse populations. For example, mean survival of adult sage-grouse increased as distance from leks to overhead lines (size or type of power line was not defined) increased within 20 km of overhead lines (Armentrout and Hall 2005). Nineteen of 20 leks in Washington, USA, within 7.5 km of multiple 500-kV transmission lines became vacant (Schroeder 2010). Landscape connectivity in Washington, in regard to gene flow and lek occupancy, was also affected by power lines (Shirk et al. 2015). In Nevada, USA, sage-grouse resource selection and demography were negatively associated with habitats ≤12.5 km from a 345-kV transmission line (Gibson et al. 2018). In addition, lek trends, nesting and brooding habitat selection, and nest and brood success were negatively correlated with power lines ≤2.8 km from power lines (Kohl et al. 2019). Whereas some researchers have documented negative relationships, others have not observed a relationship between power lines and different sage-grouse population parameters. For example, the same study in Nevada found only a weak effect of a 345-kV transmission line on adult female survival (Gibson et al. 2018). In Utah, USA, female sage-grouse with broods selected areas closer to transmission lines, but the authors acknowledged some potential confounding factors associated with this analysis (Westover et al. 2016). At the landscape scale, transmission lines did not affect lek persistence in a multi-state study (Kohl et al. 2019). There are several unique characteristics associated with each of these studies, including location, duration, seasonal timing, size of power line, and habitat characteristics, all of which have the ability to influence the interpretation of the generalized effects of transmission lines on sage-grouse populations.

We investigated potential effects of 230-kV wood pole, H-frame transmission lines on habitat selection and survival of a sage-grouse population during 3 biologically meaningful periods: nesting, brood-rearing, and summer. The objective of our study was to estimate the effects of 230-kV transmission lines on reproductive sage-grouse habitat selection and survival by accounting for local environmental conditions that could potentially confound the relationship with transmission lines in 2 different study areas. We predicted the presence of transmission lines would affect sage-grouse habitat function, but the extent and magnitude would vary based on habitat suitability.

STUDY AREA

Our study areas were located north of Interstate 80 and south of the Shirley Basin in Carbon County, Wyoming, USA, consistent with the description provided by LeBeau et al. (2017; latitude 41.91°, longitude −106.37°; Fig. 1). We separated our study area based on leks in 2 areas: the Seven Mile Hill (SMH) group consisted of 4 leks north of US Highway 30 and 287, and the Simpson Ridge (SR) group consisted of 6 leks south of US Highway 30 and 287. The average minimum distance between the SMH and SR leks was 11.7 km. We considered females from SMH area leks to occupy habitats within the SMH study area and females from the SR area leks to occupy habitats within the SR study area. We further defined each study area by calculating home ranges from the distribution of radio-marked females to define the outer boundary of each study area consistent with the description in LeBeau et al. (2017).

Multiple 230-kV wooden H-frame transmission lines occurred within each study area (Fig. 1). One transmission line bisected the SR study area east to west and 1 transmission line bisected the SMH study north to south. A portion of the transmission line at SMH was co-located with an existing county dirt road and located in the northern portion of the SMH. The transmission line that bisected the SMH study area also occurred within a small portion of the western SR study area. There were 30 km of transmission lines within SR and 31 km within SMH. The transmission lines within both study areas have existed on these landscapes for >10 years. The distance from capture lek to the nearest transmission line ranged from 3.0 km to 6.0 km at SMH and from 1.0 km to 6.4 km at SR.

METHODS

Field Methods

The main sampling units for our study were 10 occupied sage-grouse leks. From these leks, we captured female sage-grouse and monitored marked individuals through time. Leks targeted for captures were located throughout the study areas. Our field methods followed those described by LeBeau et al. (2017) where we captured 346 ($n = 160$ in SMH, 186 in SR) female sage-grouse at night roosts near leks by spotlighting and use of hoop nets (Giesen et al. 1982, Wakkinen et al. 1992) during the 2009 through 2013 breeding seasons. We classified individuals as yearling or adult (Eng 1955) and fitted each captured sage-grouse with a 22-g necklace-mounted very high frequency (VHF) radio transmitter with a battery life of 666 days (Advanced Telemetry Systems, model A4000, Isanti, MN, USA).

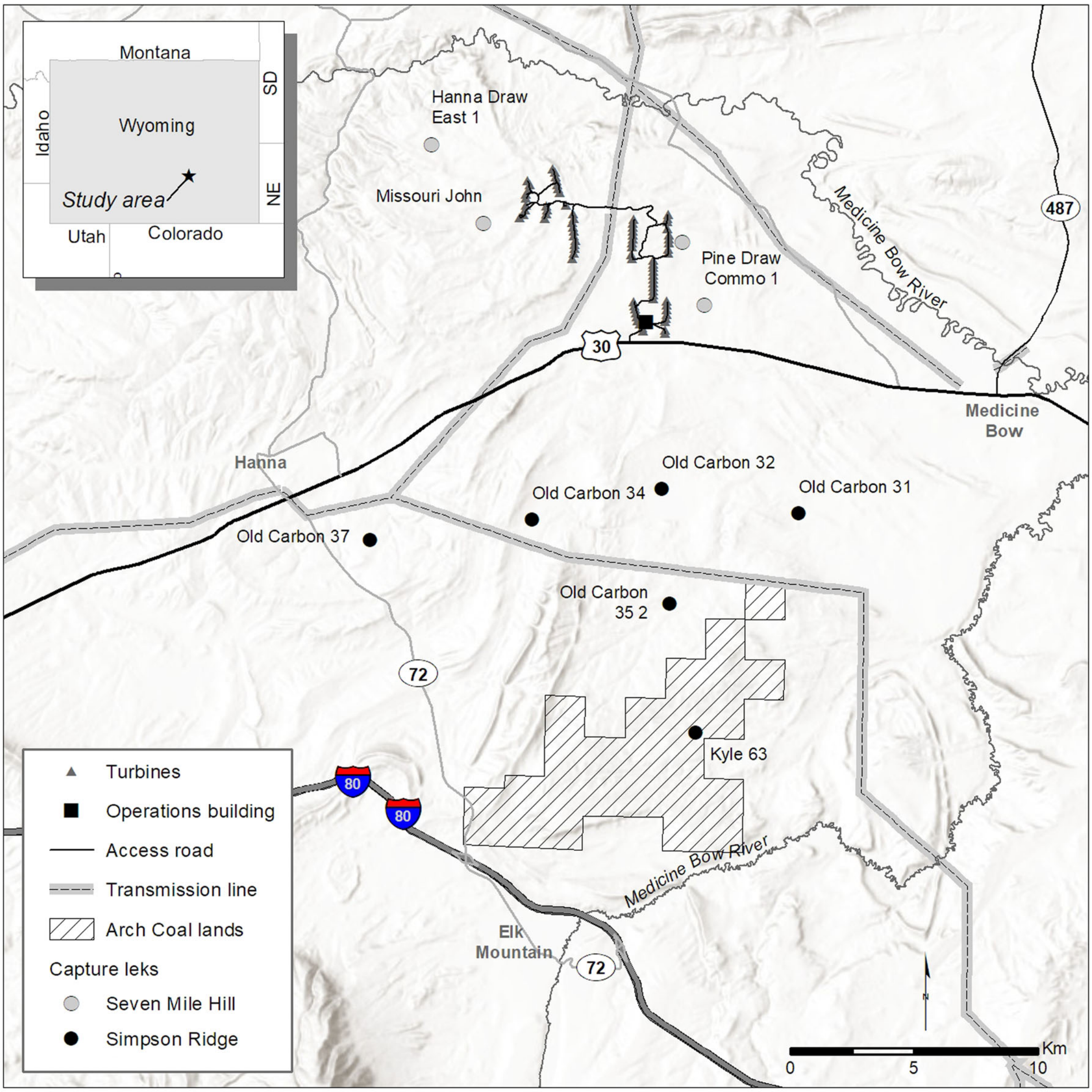

Figure 1. Location of transmission lines and occupied sage-grouse leks targeted for capture and monitoring female sage-grouse within the Seven Mile Hill and Simpson Ridge study area from 2009–2014 in Carbon County, Wyoming, USA.

Radio-transmitters were equipped with a mortality sensor that was trigged after 8 hours without movement. We obtained approval from the Wyoming Game and Fish Department (Chapter 33, permit 572) to capture, handle, and monitor female greater sage-grouse.

We attempted to locate each radio-marked female 3 times/week during the pre-nesting and nesting period (Apr through Jun); and at least once weekly for brooding and broodless females (i.e., females that were not currently nesting or raising young) from nest fate through 31 October (LeBeau et al. 2017). We monitored marked sage-grouse from the ground using hand-held receivers and antennas. We determined sage-grouse locations by triangulation or homing until marked individuals were visibly observed.

Once a nest location was established, we conducted incubation monitoring on an alternate-day schedule to determine nest fate. For each nest attempt, we collected data on timing of incubation and nest success. We considered a nest that successfully hatched (i.e., eggs with detached membranes; Wallestad and Pyrah 1974) ≥1 egg to be a successful nesting attempt (Rotella et al. 2004). Nests that failed to hatch ≥1 egg were failed nesting attempts. We mapped all nest locations using a hand-held global positioning system (GPS). We monitored females that were unsuccessful in their first nesting attempt 3 times/week through 15 June to determine possible second nesting attempts.

Geographic Information System Covariates

We developed a suite of anthropogenic, vegetation, and environmental covariates to estimate habitat selection and survival (Table 1). We digitized transmission lines and roads using aerial satellite imagery and ArcMap 10 (Environmental System Research Institute [ESRI], Redlands, CA, USA) to calculate the minimum distance to each feature. We developed a binary viewshed covariate (visible = 1 and not

Table 1. Explanatory anthropogenic and environmental covariates used in modeling sage-grouse nest, brood, and summer habitat selection and survival at the Seven Mile Hill and Simpson Ridge study areas, Carbon County Wyoming, USA, 2009–2014. We calculated percent cover at multiple scales specific to each analysis.

Covariates	Variable description
Anthropogenic infrastructure	
Distance to major roads	Distance from sage-grouse location to nearest major road (WY Highway 72, U.S. Highway 287 and 30, and I-80; km)
Distance to transmission line	Distance from sage-grouse location to nearest overhead transmission line (km)
Visible transmission line (viewshed)	A point on the landscape where a transmission line was visible to sage-grouse
Distance to turbines	Distance from sage-grouse location to nearest turbine (km)
Proportion of disturbance	% of surface disturbed by the Seven Mile Hill Wind Energy Facility (e.g., turbine pads and access roads) for each spatial scale.
Vegetation	
Bare ground	% bare ground (1-m resolution)
Big sagebrush[a]	% big sagebrush (30-m resolution)
Herbaceous	% herbaceous cover (1-m resolution)
Litter[a]	% litter (30-m resolution)
Sagebrush[a]	% sagebrush (30-m resolution)
Shrub	% shrub cover (1-m resolution)
Shrub height[a]	Shrub height (0–253 cm; 30-m resolution)
Meadow	% meadow (1-m resolution)
Distance to meadow	Distance from sage-grouse location to nearest meadow (km)
Wyoming big sagebrush[a]	% Wyoming big sagebrush (30-m resolution)
Environmental	
Slope	Degrees 0–90 (10-m resolution)
Terrain ruggedness	Variability in slope and aspect (0–1; 1 = complete terrain variation; Sappington et al. 2007; 10-m resolution)
Distance to capture lek	Distance from sage-grouse location to respective lek of capture
Distance to nearest occupied lek	Distance from sage-grouse location to nearest occupied lek
Elevation	Altitude above sea level (m; 10-m resolution)
Compound topographic index	Water accumulation (large values = high water accumulation; 10-m resolution)
Topographic position index	Variability in average elevation within a neighborhood (−1–1; Positive values = ridges; negative values = valleys; 10-m resolution)

[a] Vegetation covariates obtained from Homer et al. (2012).

visible = 0) that determined where a transmission line was visible to sage-grouse from any point on the landscape. The viewshed predictor assumed visibility from ground level without accounting for height of surrounding vegetation. We constrained our models with height above ground for the transmission line at 27 m tall and modeled the extent at which a sage-grouse could see the transmission line (i.e., viewsheds as either 0.5, 1, 1.5, 2, 2.5, or 3 km). We calculated viewsheds in ArcMap 10.

Vegetation layers used in the analysis were remotely sensed vegetation products developed from 1-m resolution National Agricultural Imagery Program (NAIP) image mosaics acquired in 2009 and 2012 (U.S. Department of Agriculture 2009, 2012; LeBeau et al. 2017) and vegetation products developed by Homer et al. (2012). We considered 4 primary continuous field components including percent bare ground, percent herbaceous cover, percent shrub cover (LeBeau et al. 2017), and percent litter (Homer et al. 2012), and 4 secondary components including percent sagebrush (*Artemisia* spp.), percent big sagebrush (*A. tridentata* spp.), percent Wyoming big sagebrush (*A. t. wyomingensis*), and shrub height (Homer et al. 2009, 2012; Table 1). We considered landscape features such as elevation, slope, compound topographic index (CTI), topographic positon index (TPI), and terrain ruggedness, all of which we calculated from a 10-m National Elevation Dataset (DEM; U.S. Geological Survey 2015). We also included distance to nearest lek (km) and distance to lek of capture (km) as covariates.

General Analysis Methods

We found evidence for variable effects of transmission lines in previous landscape-scale habitat selection and demographic analyses in our study areas (LeBeau et al. 2017). For example, sage-grouse appeared to select habitats close to transmission lines in 1 study area and avoided these habitats in the other study area during various seasonal periods. In addition, we observed a negative effect on nest survival but no effect on female survival. Therefore, we assumed that variation in behavior and demography relative to transmission lines was potentially confounded by other environmental factors (e.g., elevation, distance to lek, TPI, or a combination). To account for potential confounding factors, we followed the approach of Avgar et al. (2017) to estimate the effect of transmission lines on selection and survival, after accounting for habitat conditions other than transmission lines in our study areas. Our general approach was to first predict habitat selection and survival during each time period for each study area using models previously developed that excluded transmission line covariates. We converted those predictions to a habitat suitability index (HSI; described below) and used HSI as independent predictor variables in further modeling (models used to create the HSI are available online in Supporting Information). The HSI, therefore, incorporated several habitat covariates that could be simultaneously influencing selection and survival. We then evaluated models with the main effects of HSI and transmission line predictors and models that included interactions of HSI with transmission line covariates to evaluate potential effects of transmission lines on resource selection or survival. These final models then served as a proxy for habitat function.

Habitat Selection Analyses

We had a unique opportunity to model the effect of transmission lines in 2 different study areas simultaneously using consistent habitat data, allowing us to compare the potential relationship of transmission lines between groups of individuals with differing available habitats. We previously developed habitat selection models that estimated the relative probability of nest site, brood-rearing, and summer habitat selection within our study areas (LeBeau et al. 2017). These models followed the form of a discrete choice habitat selection models (Arthur et al. 1996, Manly et al. 2002, McDonald et al. 2006). We removed the transmission line covariates that were included in these models and re-estimated the models in our study areas to develop our base habitat selection models. Models used to create base habitat selection models are available online in Supporting Information. The coefficients from these discrete choice models yielded resource selection functions (RSFs), defined as any function that provides predictions that are proportional to the probability of use of habitat units (Manly et al. 1993, 2002). We employed a Type I study design where habitat selection and availability were estimated at the population level and over a 6-year time period (Thomas and Taylor 2006). We defined available habitat by calculating kernel home ranges for all sage-grouse locations observed from 2009–2014 within each time period for the SMH and SR study areas consistent with LeBeau et al. (2017). Yearly kernel home range sizes and extents varied slightly during the study, thus we combined locations and established available habitat from all data by study area.

We developed RSFs during 3 biologically meaningful periods: nesting, brood-rearing, and summer. We included all first and second nesting attempts from a given year in the nest site habitat selection analysis. We included all early and late brood locations (i.e., 30–35 days post-hatch) associated with each female grouse that successfully hatched ≥1 egg in the brood-rearing habitat selection analysis. We did not include subsequent locations from females that were not successful during either the early or late brood-rearing period in the brood-rearing analysis because our goal was to model selection patterns of brooding females. We included the locations of broodless females and all locations observed after the late brood-rearing period through 31 October of each year in the summer habitat selection analysis.

We generated grid cells with 90-m × 90-m spacing to identify available habitat units within each study area's available extent. We extracted covariates associated with each available habitat unit at varying scales that were included in the previously developed RSFs to include in each RSF model that did not include a transmission line effect (LeBeau et al. 2017). A choice set included all available habitat units associated with a specific nest, brood-rearing, and summer location, and the used nest, brood, or summer habitat unit. We then used these models to evaluate habitat function by considering the effect of transmission lines.

Survival Analysis

Similar to the habitat selection analysis, we created survival models by applying previously developed nest and female survival models that did not consider the effect of transmission lines within our study areas (LeBeau et al. 2017). We did not estimate brood survival relative to transmission lines because of the small number of failed broods ($n = 7$) within 2 km of transmission lines. We included random effects associated with all individuals captured at specific leks to the best approximating model to allow for random fluctuations in the baseline hazard for each individual because variation in survival could be related to the habitat associated with the lek at which a female bred (Connelly et al. 2000, Liebezeit et al. 2009). We assessed the utility of including random effects using an analysis of variance (ANOVA) and a Wald chi-square test (Therneau 2015). We excluded the random effects term from the best approximating survival model if the ANOVA test indicated no significant differences between the random effects model and the proportional hazards model with only fixed effects. We used the Andersen-Gill (A-G) formulation of the Cox model to estimate female survival because of its ability to use time-varying covariates as covariates changed throughout the survival period (Anderson and Gill 1982). There was some uncertainty in the exact time of failure as a result of our discrete monitoring methods; however, we assumed the data were continuous in our modeling and this assumption would not influence our results.

We assessed nest survival for a 28-day incubation period during the 2009 through 2014 nesting seasons (incubation period lasts 25–29 days; Schroeder et al. 1999). We combined nests observed within each study area into 1 sample to model survival relative to transmission lines because we found no differences in survival relative to study area (LeBeau et al. 2017). Nests from second attempts following failed nests for each individual might not be independent of first nests and were excluded from survival analyses. Furthermore, a range-wide assessment suggested that nest success of second nest attempts was higher than first nest attempts (Taylor et al. 2012), which could potentially bias our results. First nests that hatched in early July were considered re-nests and excluded from analyses because they were within the hatch date range of other re-nests and we assumed the first nesting attempt was likely missed by the observer. Failures occurred when a female's nest was predated. We assigned the nest's date of failure half way between the last 2 monitoring intervals. We considered nests that contained at ≥1 egg at the end of the 28-day incubation period to be successful and censored them (Nur et al. 2004).

We modeled female sage-grouse survival from time of capture or 1 April to 31 October during all study years. We monitored female sage-grouse ≥1 time/week during this period. We assumed that seasons were independent when there were multiple seasons of survival data for a single female. We recorded mortality events when we confirmed mortality visually via telemetry. We assigned the date of mortality by the condition of the carcass and last monitoring interval when the individual was known to be alive. We combined individuals into 1 sample because there was no differences in the variability of survival between the study areas (LeBeau et al. 2017).

Habitat Function

We used coefficients from base habitat selection and survival models to estimate RSFs or survival probability functions (SPFs; Kirol et al. 2015), respectively. Models took the form: $w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots \beta_k x_k)$, where β_1, β_2, β_k were coefficients of $x_1, x_2, \ldots x_k$ covariates. We transformed each RSF and SPF to an HSI, $\mathrm{HSI} = w(x)/[1 + w(x)]$, to scale relative predictions between zero and 1 to compare multiple RSFs and SPFs.

We fit a second set of models for each behavior and demographic rate by interacting predicted HSI values and 1 transmission line covariate (distance to or visual transmission; Table 1). If a transmission line was influencing habitat selection or survival, we expected a model containing a transmission line covariate to be the most parsimonious model when compared to the model that only included HSI. We considered the most parsimonious model to be the model with the lowest corrected Akaike's Information Criterion (AIC_c; Akaike 1974, Burnham and Anderson 2002). A significant interaction (alpha level = 0.10) between transmission line and HSI would suggest that the relationship between transmission line and selection or survival varied with HSI. We created marginal effects plots to visually inspect the relative probability of selection or survival associated with transmission line covariates.

We used k-fold cross-validations to evaluate the predictive ability of each RSF that informed habitat function (Boyce et al. 2002). We partitioned used habitat units and respective choice sets into 5 equal-sized groups, removed 1 group (testing data) and re-estimated coefficients in each RSF model with the remaining groups (testing data). We then used coefficients from testing data models to generate predictions with testing data. We binned predictions within each choice set into 20 equal size percentile classes. We compared the number of used habitat units from all choice sets in each prediction class to binned class ranks using a Spearman's rank correlation. We repeated this process for each group and averaged Spearman's rank correlation coefficients (r_s) to test model performance.

Once we developed and validated RSFs and SPFs, we evaluated the relative probability of selection and survival during the different study periods and study areas to assess potential effects of transmission lines on habitat function. We placed a 90-m × 90-m grid within the extent of combined home ranges within both study areas to create predictive surfaces. Individual pixels with lower relative probability of use or survival were suggested to have low habitat function relative to pixels with high relative probability of use or survival. There were 3 covariates used in base models with values that changed from 2009–2011 to 2012–2014; thus, we generated predictive surfaces for each period. We averaged all the RSF and SPF predictive surfaces separately to get an average prediction for habitat selection and survival. We then averaged the habitat selection and survival predictions to estimate habitat function scores.

We then determined the distance from transmission lines at which habitat function was lowest. We evaluated habitat function relative to transmission lines and occupied leks across varying levels of HSI. We placed the HSI predictions into 3 equal-area bins (i.e., low, medium, high) using percentiles to represent habitats with progressively higher HSI predictions. We estimated thresholds or change points for each HSI percentile relative to transmission lines with a recursive partitioning approach with the change point defined as the first node of a classification tree for each HSI category (Qian et al. 2003). We determined the threshold using the rpart package in R (Therneau et al. 2019, R Core Team 2016). This method estimates the point resulting in the largest deviance reduction in the average habitat function score (e.g., average prediction) from all predicted surfaces. We resampled the habitat function scores from all predicted surfaces with replacement 100 times to attain bootstrap confidence intervals for the threshold using the percentile method (Qian et al. 2003, Manly 2006). We judged the significance of threshold results with a chi-square test of significance having 1 degree of freedom. We rejected the null hypothesis of no change point if the threshold identified by recursive partitioning was better than a null model with no threshold. We plotted habitat function for low and high HSI relative to distance to transmission line to visually inspect the results. In addition, we determined the average distance of pixels within each percentile bin to occupied leks to inform management recommendations.

RESULTS

The most parsimonious models for nest site selection at SR and SMH included an interaction between HSI and visible transmission line with a 1.5-km sage-grouse viewshed and an interaction between HSI and a quadratic effect of distance to transmission line, respectively (Table 2). However, we detected a significant interaction only between the visible transmission line covariate with a 1.5-km viewshed and HSI at SR (Table 3). In habitats with lower HSI predictions at SR (e.g., <0.6), the relative probability of nest site selection in visible and non-visible habitats were similar (Table 3; Fig. 2). As HSI increased, however, the relative probability of nest site selection increased in habitats that were not visible to transmission lines, suggesting females avoided selecting nests sites that were visible to transmission lines in habitats with higher suitability (Fig. 2). Visual inspection of partial plots suggested that relative probability of nest site selection at SMH increased as distance to transmission line increased to approximately 3.5 km before decreasing in high HSI habitats, providing some evidence of avoidance in high HSI habitats when sage-grouse are close to the transmission line (Fig. 3A). The

Table 2. Top 10 sage-grouse habitat selection models at the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009–2014. Model fit statistics include number of parameters (K), corrected Akaike's Information Criterion (AIC_c), change in AIC_c (ΔAIC_c), and Akaike weights (w_i). We included the habitat suitability index (HSI) base model if it was not within the top 10 habitat selection models. The transmission covariate included the linear distance to the nearest transmission line and the viewshed covariate determined if the transmission line was visible to sage-grouse assuming various distances at which the sage-grouse could see the transmission line.

Model	K	AIC_c	ΔAIC_c	w_i
Simpson Ridge nest site selection				
HSI × viewshed (1.5 km)	4	3,331.49	0.00	1.00
HSI × viewshed (2.0 km)	4	3,335.91	4.42	0.11
HSI + transmission	3	3,337.82	6.33	0.04
HSI + viewshed (2.0 km)	3	3,337.82	6.34	0.04
HSI × viewshed (2.5 km)	4	3,338.16	6.67	0.04
HSI + viewshed (1.5 km)	3	3,338.49	7.00	0.03
HSI × transmission + HSI × transmission^2	6	3,339.03	7.54	0.02
HSI × transmission	4	3,339.38	7.89	0.02
HSI + transmission + transmission^2	4	3,339.74	8.26	0.02
HSI × viewshed (3.0 km)	4	3,340.07	8.58	0.01
HSI	2	3,343.68	12.20	0.00
Seven Mile Hill nest site selection				
HSI × transmission + HSI × transmission^2	6	2,716.14	0.00	0.61
HSI + transmission + transmission^2	4	2,717.06	0.02	0.39
HSI × viewshed (1.0 km)	4	2,751.58	35.45	0.00
HSI × viewshed (0.5 km)	4	2,757.17	41.03	0.00
HSI × viewshed (3.0 km)	4	2,759.62	43.48	0.00
HSI + viewshed (3.0 km)	3	2,761.45	45.32	0.00
HSI × viewshed (1.5 km)	4	2,761.91	45.78	0.00
HSI × viewshed (2.0 km)	4	2,762.48	46.35	0.00
HSI + viewshed (2.5 km)	3	2,762.58	46.44	0.00
HSI × viewshed (2.5 km)	4	2,763.65	47.51	0.00
HSI	2	2,772.94	56.80	0.00
Simpson Ridge brood-rearing habitat selection				
HSI + transmission + transmission^2	4	9,137.10	0.00	0.75
HSI × transmission + HSI × transmission^2	6	9,139.32	2.22	0.25
HSI × transmission	4	9,156.53	19.43	0.00
HSI + transmission	3	9,179.77	42.67	0.00
HSI + viewshed (0.5 km)	3	9,181.20	44.10	0.00
HSI × viewshed (0.5 km)	4	9,182.39	45.29	0.00
HSI + viewshed (2.0 km)	3	9,184.39	47.29	0.00
HSI + viewshed (1.5 km)	3	9,185.82	48.72	0.00
HSI × viewshed (2.0 km)	4	9,185.94	48.84	0.00
HSI	2	9,186.97	49.87	0.00
Seven Mile Hill brood-rearing habitat selection				
HSI + transmission + transmission^2	4	7,364.41	0.00	0.76
HSI × transmission + HSI × transmission^2	6	7,366.76	2.34	0.24
HSI × viewshed (1.0 km)	4	7,397.18	32.77	0.00
HSI × viewshed (0.5 km)	4	7,397.48	33.07	0.00
HSI × viewshed (2.0 km)	4	7,406.67	42.26	0.00
HSI + viewshed (1.0 km)	3	7,406.71	42.30	0.00
HSI + viewshed (0.5 km)	3	7,407.66	43.25	0.00
HSI + viewshed (2.0 km)	3	7,410.48	46.07	0.00
HSI × viewshed (1.5 km)	4	7,412.26	47.84	0.00
HSI + viewshed (1.5 km)	3	7,414.20	49.78	0.00
HSI	2	7,433.18	68.76	0.00
Simpson Ridge summer habitat selection				
HSI × transmission + HSI × transmission^2	6	35,327.38	0.00	0.92
HSI + transmission	3	35,333.31	5.93	0.04
HSI × transmission	4	35,335.31	7.75	0.02
HSI + transmission + transmission^2	4	35,335.31	7.93	0.02
HSI + viewshed (3.0 km)	3	35,352.15	24.77	0.00
HSI + viewshed (2.5 km)	3	35,354.02	26.64	0.00
HSI × viewshed (3.0 km)	4	35,354.15	26.77	0.00
HSI × viewshed (2.5 km)	4	35,355.80	28.42	0.00
HSI + viewshed (2.0 km)	3	35,360.72	33.34	0.00
HSI × viewshed (2.0 km)	4	35,362.54	35.16	0.00
HSI	2	35,385.90	58.52	0.00
Seven Mile Hill summer habitat selection				
HSI + transmission + transmission^2	4	31,543.65	0.00	0.45
HSI + viewshed (3.0 km)	3	31,544.70	1.05	0.26
HSI × viewshed (3.0 km)	4	31,545.55	1.90	0.17
HSI × transmission + HSI × transmission^2	6	31,546.32	2.67	0.12

(*Continued*)

Table 2. (*Continued*)

Model	K	AIC$_c$	ΔAIC$_c$	w_i
HSI × viewshed (2.5 km)	4	31,559.77	16.12	0.00
HSI + viewshed (2.5 km)	3	31,561.48	17.83	0.00
HSI + transmission	3	31,563.80	20.15	0.00
HSI × transmission	4	31,565.67	22.02	0.00
HSI × viewshed (2.0 km)	4	31,577.12	33.47	0.00
HSI + viewshed (2.0 km)	3	31,578.30	34.65	0.00
HSI	2	31,590.86	47.21	0.00

5-fold validation indicated that RSF models developed at SMH and SR had moderate overall predictability ($\bar{x}\ r_s = 0.66$ and $\bar{x}\ r_s = 0.56$, respectively).

The most parsimonious models for brood-rearing habitat selection at SR and SMH both included a quadratic effect of transmission line (Table 2). Top models did not contain interactions between transmission line covariates and HSI at both study areas, suggesting no clear relationship of brood-rearing habitat selection relative to transmission lines across differing HSI values (Table 3). The relative probability of brooding rearing selection increased as distance to transmission line increased up to 4 km and 2.5 km before decreasing at SMH and SR, respectively. The 5-fold validation indicated that RSF models had good overall predictability (SMH $\bar{x}\ r_s = 0.87$, SR $\bar{x}\ r_s = 0.88$)

Similar to brood-rearing, the most parsimonious models for summer habitat selection at SR and SMH included quadratic effects of transmission lines (Table 2). Only SR models, however, contained an interaction between the quadratic effect of transmission lines and HSI during summer (Table 3). The relative probability of summer habitat selection at SR increased as distance to transmission line increased in habitats with high HSI, suggesting females selected summer habitats farther from transmission lines in high HSI habitats and transmission lines did not affect selection patterns in lower HSI habitats (Fig. 3B). The 5-fold validation indicated that RSF models developed at SMH and SR had good overall predictability ($\bar{x}\ r_s = 0.98$ and $\bar{x}\ r_s = 0.92$, respectively).

We observed 187 failed nesting attempts. Mammalian and avian predators were the main source of nest failures. The median distance to transmission lines from all successful nests (2.89 km) was similar to all failed nesting attempts (3.33 km). We used 302 first nesting attempts in the Cox proportional hazard modeling. The most parsimonious model for nest survival included an interaction between HSI and visible transmission line covariate with a 1.0-km sage-grouse viewshed (Table 4). The addition of lek of capture included as a random intercept term in the top model was not different from the model that excluded the random intercept term ($P = 0.30$). The relative probability of nest survival increased in habitats visible to transmission lines with increasing HSI, suggesting the magnitude of the effect of transmission lines on nest survival was greatest in habitats with lower habitat suitability and lowest in habitats with high suitability (Table 5; Fig. 4). Habitat suitability does not appear to influence nest survival when sage-grouse are using habitats that are not visible to transmission lines (Fig. 4).

We monitored 340 females during the summer period from 2009–2014. We observed 189 mortalities of sage-grouse during the study period. There were 14 instances where the radio-transmitter possibly fell off the female and we censored those individuals at the time and location of their last known location prior to discovery. In addition, we removed 5 mortalities from the analysis that were potentially related to the stress of capture and handling because these mortalities were recorded within 10 days of capture (Kurzejeski et al. 1987). Most mortalities (56.1%) occurred during the first 10 weeks of summer (1 Apr through 10 Jun). It was difficult to accurately determine cause of female mortality; however, most mortalities were likely attributed to avian predators because females are more effective at evading mammalian predators (Conover et al. 2010).

We used 6,378 locations, 31 monitoring intervals, and 511 female-years (340 individuals monitored across multiple years) to model female summer survival relative to transmission lines over the study period. We included year as a stratum in the A-G model to allow different baseline hazards each year. The most parsimonious model for female survival included the main effects of HSI and visible transmission lines with a 0.5-km sage-grouse viewshed (Tables 4 and 5). The addition of lek of capture included as a random intercept term in the top model was not significantly different from the model that excluded the random intercept term ($P = 0.97$). Risk of mortality was 1.4 times higher in habitats that were visible to transmission lines assuming a 0.5-km sage-grouse viewshed (Table 5).

We found evidence to suggest that the presence of the transmission lines reduced habitat function and the magnitude of this effect varied based on habitat suitability. By incorporating predictions from these models, we determined that the reduction in habitat function due to the presence of transmission lines was greater in habitats with higher suitability compared to habitats with lower suitability (Fig. 5). Habitats with high suitability within 0.95 km (90% CI = 0.949 – 0.962 km) of a transmission line were associated with lower survival and lower relative probability of use when we combined the habitat selection and demography results to evaluate habitat function (Fig. 6). The magnitude of the effect of transmission lines on habitat function was lower in habitats with lower suitability within 0.50 km (90% CI = 0.495–0.780 km; Fig. 6). We rejected the hypothesis of

Table 3. Coefficients and 90% confidence intervals associated with covariates included in the most parsimonious model for nest, brood-rearing, and summer habitat selection by sage-grouse at the Simpson Ridge (SR) and Seven Mile Hill (SMH) study areas, Carbon County, Wyoming, USA, 2009–2014. The habitat suitability index (HSI) covariate was the relative probability of habitat selection without the influence of transmission line. The transmission covariate included the linear distance to the nearest transmission line and the viewshed covariate determined if the transmission line was visible to sage-grouse assuming various distances at which the sage-grouse could see the transmission line.

	Nest site selection		Brood-rearing habitat selection		Summer habitat selection	
Covariate	**SMH**	**SR**	**SMH**	**SR**	**SMH**	**SR**
HSI	4.41 (−0.46, 9.29)	5.71 (4.63, 6.79)	10.15 (9.01, 11.30)	6.02 (5.50, 6.54)	4.95 (4.69, 5.21)	4.83 (4.16, 5.49)
Transmission	−0.69 (−4.19, 2.80)		0.72 (0.55, 0.89)	−0.15 (−0.22, −0.08)	−0.24 (−0.31, −0.18)	−0.55 (−0.89, −0.21)
Transmission^2	−0.10 (−0.71, 0.51)		−0.09 (−0.11, −0.07)	0.03 (0.02, 0.03)	0.02 (0.01, 0.03)	0.10 (0.05, 0.15)
Viewshed (1.5 km)		2.31 (1.28, 3.35)				
HSI × transmission	2.35 (−1.38, 6.09)					0.89 (0.44, 1.34)
HSI × transmission^2	−0.11 (−0.76, 0.54)					−0.14 (−0.21, −0.08)
HSI × viewshed (1.5 km)		−2.98 (−4.60, −1.37)				

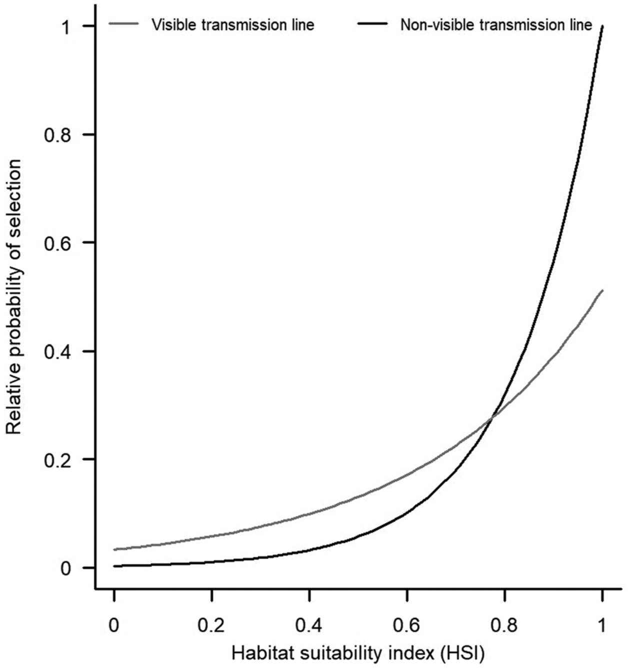

Figure 2. Probability of nest site selection relative to the visible transmission line covariate across levels of habitat suitability within sage-grouse home ranges at Simpson Ridge from 2009–2014 in Carbon County, Wyoming, USA.

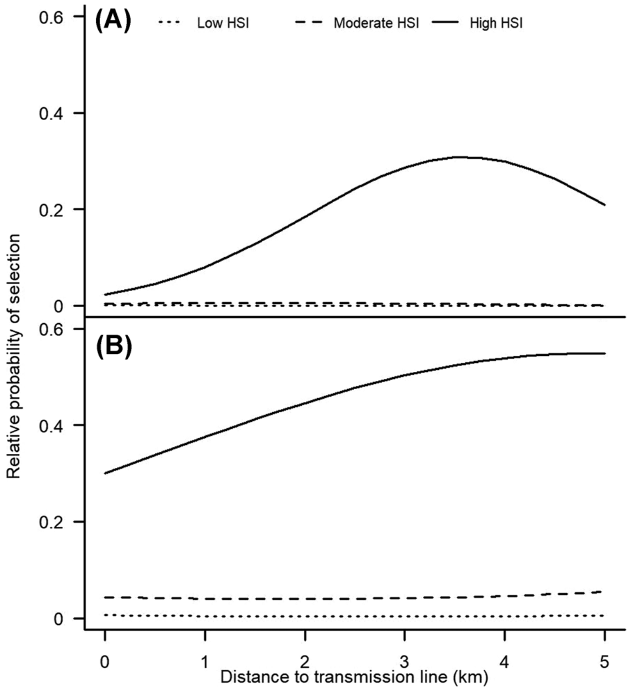

Figure 3. Probability of selection relative to the distance to transmission line covariate across low (0.1), moderate (0.5), and high (0.9) levels of habitat suitability index (HSI) within sage-grouse home ranges at Seven Mile Hill during the nesting period (A) and at Simpson Ridge during the summer (B) period from 2009–2014 in Carbon County, Wyoming, USA.

no change point because the threshold identified was better than the null model with no threshold ($P \leq 0.001$). In contrast, habitat function without the influence of transmission lines in habitats with high and low suitability did not experience a change point, providing further evidence that the presence of the transmission lines decreased habitat function (Fig. 5).

DISCUSSION

We examined habitat selection and survival to evaluate the effects of 230-kV transmission lines on female sage-grouse during the nesting, brood-rearing, and summer periods while accounting for potential confounding factors. Although the transmission lines we studied were the same voltage and configuration, the relative probability of habitat selection varied during different time periods and between study areas (LeBeau et al. 2017). Overall, transmission lines were negatively correlated with sage-grouse habitat selection and survival within our study areas over 6 years. By incorporating habitat conditions into 1 metric (i.e., HSI) and the variation in habitat suitability relative to

Table 4. Top 10 models for nest and female sage-grouse survival models at the Seven Mile Hill and Simpson Ridge study areas, Carbon County, Wyoming, USA, 2009–2014. Model fit statistics include number of parameters (*K*), corrected Akaike's Information Criterion (AIC_c), change in AIC_c (ΔAIC_c), and Akaike weights (w_i). The habitat suitability index (HSI) covariate was the relative probability of survival without the influence of transmission line. The transmission covariate included the linear distance to the nearest transmission line and the viewshed covariate determined if the transmission line was visible to sage-grouse assuming various distances at which the sage-grouse could see the transmission line.

Model	K	AIC_c	ΔAIC_c	w_i
Nest survival				
HSI × viewshed (1.0 km)	4	1,308.60	0.00	0.33
HSI × viewshed (1.5 km)	4	1,309.01	0.41	0.27
HSI + viewshed (1.5 km)	3	1,309.64	1.04	0.20
HSI + viewshed (0.5 km)	3	1,312.89	4.29	0.04
HSI + transmission + transmission^2	4	1,313.11	4.51	0.03
HSI + viewshed (1.0 km)	3	1,313.16	4.56	0.03
HSI × viewshed (0.5 km)	4	1,314.86	6.26	0.01
HSI + viewshed (2.0 km)	3	1,315.11	6.51	0.01
HSI + transmission	3	1,315.20	6.60	0.01
HSI × transmission + HSI × transmission^2	6	1,315.69	7.09	0.01
HSI	2	1,316.36	7.76	0.01
Female survival				
HSI + viewshed (0.5 km)	3	1,314.03	0.00	0.46
HSI × viewshed (0.5 km)	4	1,314.43	0.41	0.37
HSI + viewshed (1.0 km)	3	1,319.11	5.08	0.04
HSI + viewshed (3.0 km)	3	1,319.98	5.95	0.02
HSI × viewshed (1.0 km)	4	1,321.09	7.07	0.01
HSI	2	1,321.19	7.17	0.01
HSI + viewshed (1.5 km)	3	1,321.26	7.23	0.01
HSI + viewshed (2.5 km)	3	1,321.39	7.36	0.01
HSI × transmission	4	1,321.72	7.70	0.01
HSI × viewshed (3.0 km)	4	1,321.82	7.79	0.01

Table 5. Coefficients and 90% confidence intervals associated with covariates included in the most parsimonious nest and female survival models for sage-grouse at the Simpson Ridge and Seven Mile Hill study areas, Carbon County, Wyoming, USA, 2009–2014. The habitat suitability index (HSI) covariate was the relative probability of survival without the influence of transmission line. The viewshed covariate determined if the transmission line was visible to sage-grouse assuming various distances at which the sage-grouse could see the transmission line.

Covariate	Nest survival	Female survival
HSI	5.23 (3.11, 7.34)	4.80 (3.76, 5.83)
Viewshed (0.5 km)		0.89 (0.45, 1.33)
Viewshed (1.0 km)	5.31 (2.37, 8.26)	
HSI × viewshed (1.0 km)	−9.62 (−15.54, −3.70)	

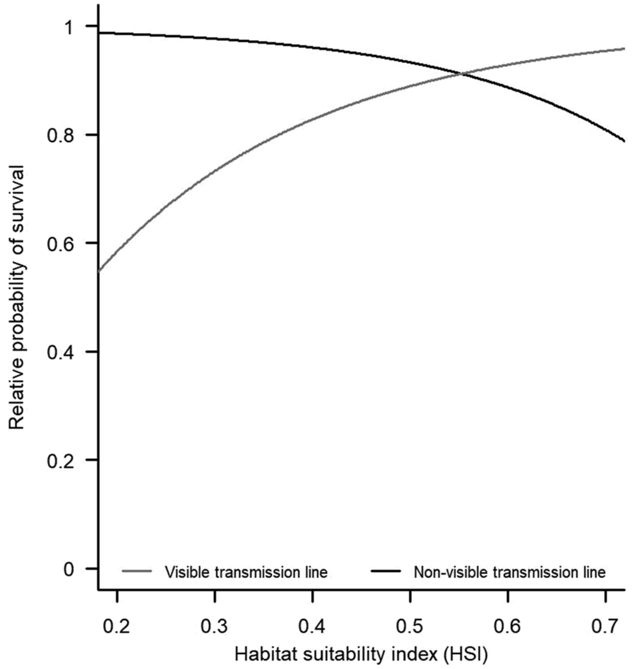

Figure 4. Relative probability of sage-grouse nest survival compared to the habitat suitability index (HSI) when transmission lines were either visible or not visible at the Seven Mile Hill and Simpson Ridge study areas from 2009–2014 in Carbon County, Wyoming, USA.

transmission lines, we obtained consistent results between SMH and SR. Our interpretation that sage-grouse avoided habitats close to transmission lines at SMH and selected habitats closer to transmission lines at SR in LeBeau et al. (2017) was likely confounded by the extent of available habitat and habitat features on the landscape and not the presence of the transmission lines. The few studies that have estimated the effects of transmission lines on sage-grouse habitat selection generally reported that habitat selection was not influenced by transmission lines, but the authors acknowledged some potential confounding issues (Wisinki 2007, Hansen et al. 2016, Westover et al. 2016). Kohl et al. (2019) did detect avoidance during the nesting and brooding season, but the magnitude of avoidance depended on the availability of sagebrush cover and possible correlation of power lines and roads. By incorporating habitat suitability in our analysis, we were able to estimate the effect of transmission lines in habitats with varying habitat suitability, addressing a potential issue confounding previous results. Further, because the base models used to estimate HSI included other anthropogenic stressors (e.g., wind turbines; Table 1), the potential confounding issues with these infrastructures were accounted for in our approach.

We found that habitat close to the transmission line may be of low suitability regardless of the presence of the transmission line (e.g., greater percentage of bare ground, close to major roads); therefore, low habitat function could be attributed to low suitability and not the presence of the transmission line. On the other hand, if habitat had high suitability and we observed an effect of transmission line, we attributed that effect to the transmission line and not the underlying habitat suitability. We consistently found the magnitude of the effect of transmission lines on habitat function to be greater in habitats with higher habitat suitability, suggesting transmission lines are negatively associated with habitat function. Nest survival was the only demographic rate we evaluated that was negatively associated with transmission lines in habitats with low suitability, suggesting that nest survival in high suitability habitats was less affected by the presence of transmission lines and possibly influenced more by habitat conditions, which was similar to Kohl et al. (2019). These transmission lines have existed on the landscape prior to our study; thus, sage-grouse

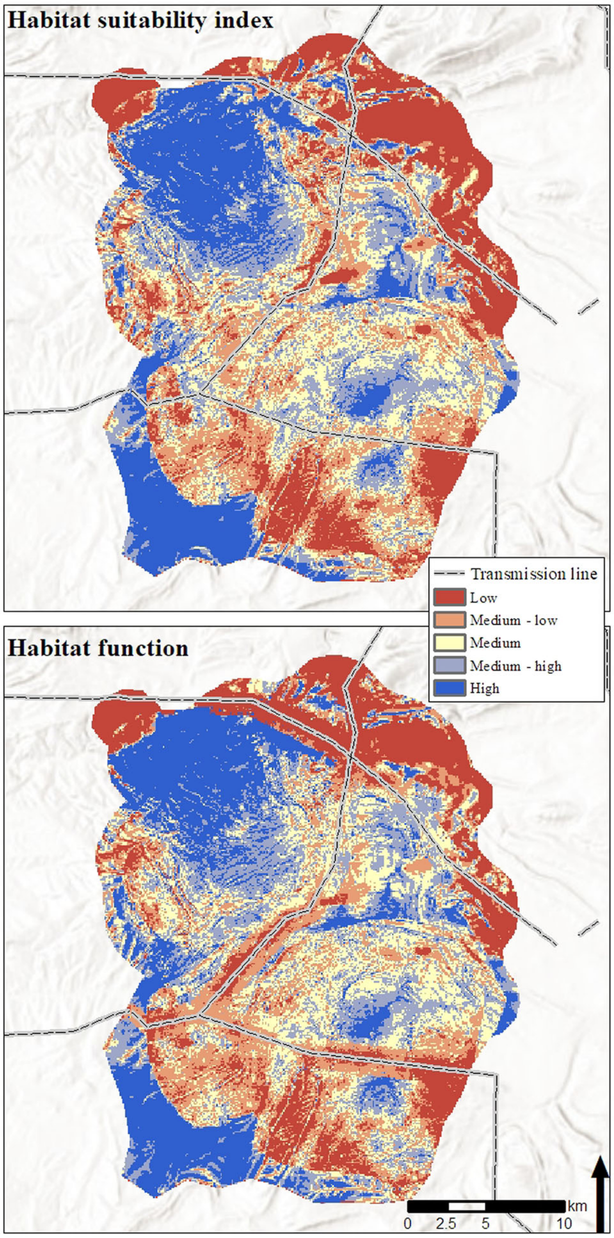

Figure 5. Predictive maps developed from resource selection and survival probability functions without the effect of transmission lines (habitat suitability index) and with the effect of transmission lines (habitat function) within sage-grouse home ranges during nesting, brood-rearing, and summer seasons combined at the Seven Mile Hill and Simpson Ridge study areas from 2009–2014 in Carbon County, Wyoming, USA.

were likely already selecting habitats relative to transmission lines, which could have influenced our estimates of habitat suitability. Nonetheless, we found clear differences in selection for transmission lines across different habitat suitability categories, suggesting we accurately captured habitat function relative to existing transmission lines.

Our results could have been strengthened with pre-construction data allowing for a before-after, control-impact (BACI) analytical approach or data from a control area in a control-impact study design (Green 1979). Many of the potential long-term effects of the transmission line may have already been realized on this sage-grouse population because it has existed on the landscape for >10 years (Johnson et al. 2011) resulting in our measuring the residual effects of the line. We benefited, however, from a long-term dataset that allowed us to detect small changes in population parameters relative to transmission lines.

Similar to other forms of anthropogenic disturbance, transmission lines may fragment the landscape, with the degree of fragmentation likely dependent on power line size (e.g., 69-kV vs. 500-kV), structure configuration (e.g., monopole vs. steel lattice), and placement on the landscape. Our results suggest that placing a 230-kV transmission line in lower suitability habitats that are not visible to sage-grouse may reduce the negative effects on habitat selection and survival. It is unknown, however, how both smaller power lines (distribution and transmission voltages) and larger transmission lines >230 kV may affect habitat selection and survival patterns, particularly given other variables, such as topography, habitat value, and predator-prey relationships within our study. We developed habitat suitability models using covariates that are important to sage-grouse populations and that were specific to this population. In general, on average, habitat suitability (e.g., 67–100% HSI) was highest within 3.14 km (90% CI = 3.14–3.16 km) of occupied leks, suggesting habitats close to leks have relatively higher suitability than those farther from leks. Kohl et al. (2019) recommended a buffer of 2.3–2.8 km from active leks to minimize the effects of new transmission lines on the population; this buffer was similar to the area we determined to have high suitability and the area where impacts are expected to be the greatest.

The mechanisms influencing habitat function relative to transmission lines are generally unknown; however, decreased habitat function could be related to the perceived threat of raptor perching (avoidance) or a higher density of predators (reduced survival; Gibson et al. 2018). Transmission lines may increase edge effects, which could increase predator efficiency (Batary and Baldi 2004). In addition, nests appeared to be more susceptible to failure in habitats visible to transmission lines with low habitat suitability, suggesting the presence of the transmission lines may have been facilitating increased predation rates in these sub-optimal habitats. Conversely, in habitats with high suitability, the presence of the transmission lines did not appear to influence nest survival potentially because the conditions in the underlying habitat were negating any advantage that transmission lines provided predators. A concurrent avian use study indicated that avian predator presence (raptors and corvids) in habitats with high suitability was greater closer to transmission lines, suggesting that higher avian predator density close to the transmission lines may have contributed to the reduction in habitat function we observed (C. W. LeBeau, Western EcoSystems Technology, Inc., unpublished data). Kohl et al. (2019) also documented high avian predator use of power lines in their study, which could have increased predation risk closer to power lines.

To our knowledge, only 3 previous studies have investigated sage-grouse nest and female survival relative to

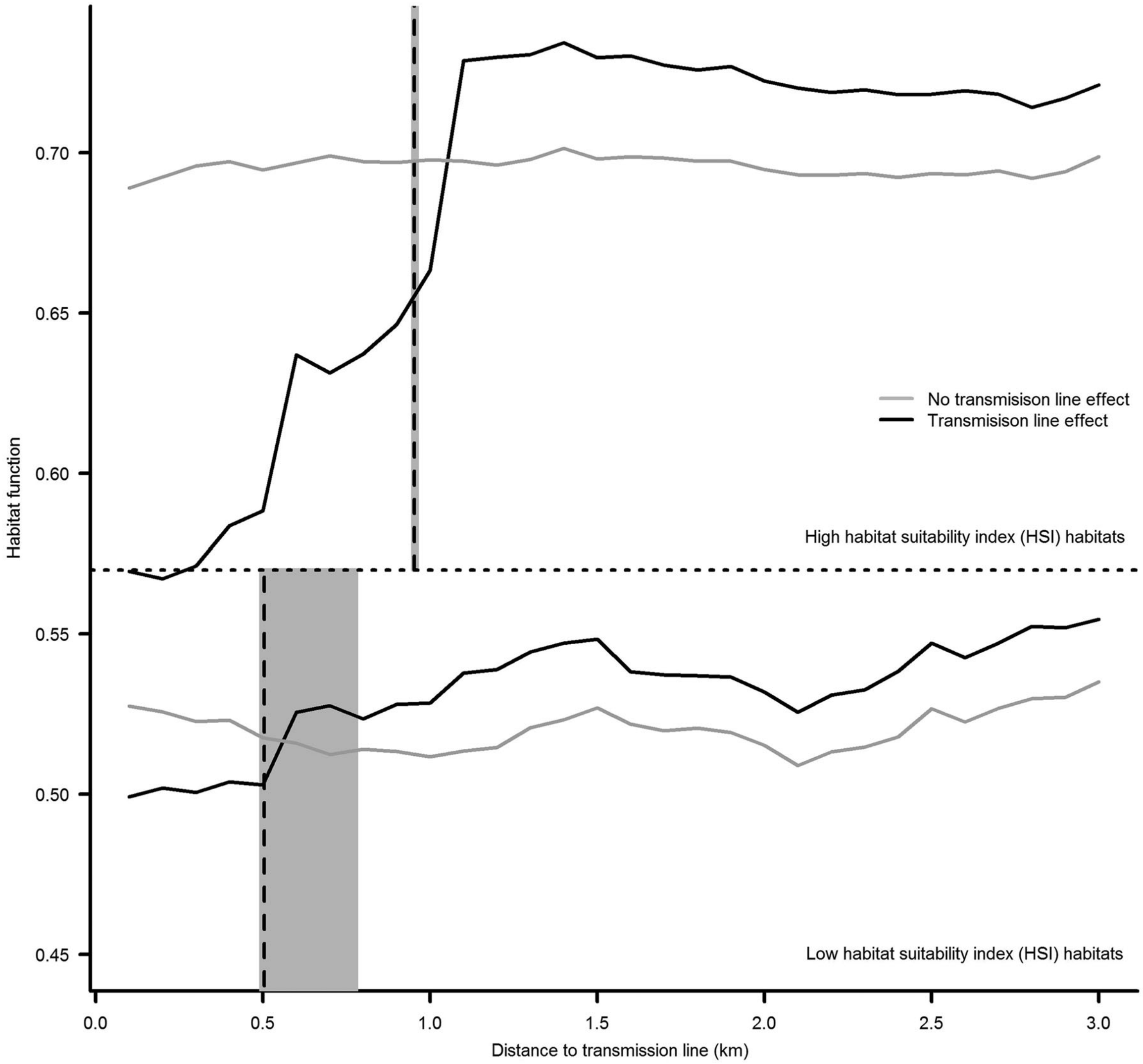

Figure 6. Sage-grouse habitat function within 3 km of transmission lines at the Seven Mile Hill and Simpson Ridge study areas from 2009–2014, Carbon County, Wyoming, USA within habitats that have a high (67–100%) and low (0–33%) habitat suitability index (HSI). Habitat function was the average relative probability of use and survival estimated during different time periods and different survival parameters. Habitats to the left the dotted line were associated with lower habitat function (e.g., low use and low survival) compared to habitats right of the dotted line when the effect of transmission lines were considered. The lower and upper 90% confidence interval bands are presented as the gray shaded areas.

transmission lines (Armentrout and Hall 2005, Gibson et al. 2018, Kohl et al. 2019). Like our study, these studies detected negative effects of the transmission lines on nest and female survival; however, the extent and magnitude of these effects varied between studies. This variation may relate to characteristics of each of these populations and to the characteristics of the power lines potentially affecting each population. In addition, differences could be related to the juxtaposition of transmission lines relative to other habitat features or predator density, which may have created confounding issues as we found in our study.

Our viewshed covariate assumed that the proximity of transmission lines has no effect on sage-grouse habitat selection and survival in habitats where transmission lines are not visible to sage-grouse. This was based on our hypothesis that if sage-grouse cannot see the transmission line then there are no mechanisms for avoidance and survival is not affected because they are less visible to avian predators perching on the transmission line. It also assumed that distances at which sage-grouse are influenced by visible transmission lines are restricted at 0.5, 1.0, 1.5, 2, 2.5, and 3 km. As we increased the sage-grouse viewshed, we essentially increased the potential magnitude of the effect of a transmission line on habitat selection and survival. By including 6 different viewsheds in our analysis, we were able to capture the extent to which a visible transmission line may be influencing sage-grouse and therefore we identified the spatial magnitude of the effect of transmission lines on habitat selection and survival. The viewshed covariates were comparable to linear distances to transmission lines; 86–93% of all habitats were in areas where transmission lines were visible. The models including viewsheds consistently outperformed HSI-only models and in many cases were similar to distance to transmission line models, suggesting that visibility of the transmission line to sage-grouse may be influencing habitat function.

The predicted surfaces allowed us to combine habitat selection and survival to determine the magnitude and extent of the transmission line effect. We assumed all time periods and survival parameters were equally important to the sustainability of this sage-grouse population, when in fact female survival may be more important to population viability than habitat use or nest survival (Taylor et al. 2012). Our goal, however, was to summarize the different effects of the transmission lines during different time periods into a single parameter that would be useful for management. We found evidence to suggest that habitats with high suitability (e.g., <3.1 km of an occupied lek) within 1.0 km of a transmission line were associated with lower survival and lower relative probability of habitat selection. Furthermore, habitats that were lower in habitat suitability (e.g., >3.1 km of an occupied lek) within 0.5 km of a transmission line were also associated with lower survival and relative probability of habitat selection.

MANAGEMENT IMPLICATIONS

The siting and design of the transmission lines in our study areas resulted in negative effects on the sage-grouse population. When designing future transmission lines, managers should avoid siting transmission lines in suitable sage-grouse habitat to ensure habitats remain intact. Recognizing this may not be possible based on our current energy demand, effects on sage-grouse populations may be minimized by siting transmission lines beyond 3.1 km from occupied leks. In addition, managers should consider monopole structure types with perch deterrents that reduce the potential for avian predator nesting and perching substrate. If effects associated with future 230-kV transmission lines cannot be avoided, the magnitude of reduction in habitat function can be quantified by summing up the size of the area within 0.5 km of transmission lines beyond 3.1 km of occupied leks and within 1.0 km of transmission lines within 3.1 km of occupied leks to determine the number of functional hectares of habitat lost due to the presence of the transmission line.

ACKNOWLEDGMENTS

We thank Hi-Allen Ranch, and PacifiCorp Energy for allowing us access to the study areas. We appreciate field assistance provided by J. Eddy, A. Hansen, P. Hansen, R. Hay, T. Higgins, M. Karsch, A. Kircher, J. Loos, A. Malone, J. Parson, T. Rintz, M. Salava, G. Shedd, B. Smith, and E. Vasquez. We thank J. Dahlke for providing project management support. We thank L. Neilson for reviewing this manuscript. We thank S. Howlin and T. McDonald for assisting in the analysis. We also thank the Associate Editor and 2 anonymous reviewers for helpful comments that improved our paper. We thank the Avian Power Line Interaction Committee, National Wind Coordinating Collaborative and Sage-Grouse Research Collaborative, American Wind Energy Association, Bates Hole-Shirley Basin Sage-grouse Local Working Group, EDP Renewables North America (formerly Horizon Wind Energy), Iberdrola Renewables, Margaret and Sam Kelly Ornithological Research Fund, PacifiCorp Energy, South-Central and Southwest Wyoming Sage-grouse Local Working Groups, United States Department of Energy, University of Wyoming Agricultural Experiment Station, University of Wyoming School of Energy Resources, and the Wyoming Reclamation and Restoration Center for providing funding support.

LITERATURE CITED

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19:716–723.

Anderson, P. K., and R. D. Gill. 1982. Cox's regression model for counting processes: a large sample study. Annals of Statistics 10:1100–1120.

Armentrout, D. J., and F. Hall. 2005. Conservation strategy for sage-grouse (*Centrocercus urophasianus*) and sagebrush ecosystems within the Buffalo-Skedaddle population management unit, Bureau of Land Management. Eagle Lake Field Office, Susanville, California, USA.

Arthur, S. M., B. F. J. Manly, L. L. McDonald, and G. W. Garner. 1996. Assessing habitat selection when availability changes. Ecology 77: 215–227.

Avgar, T., S. R. Lele, J. L. Keim, and M. S. Boyce. 2017. Relative selection strength: quantifying effect size in habitat and step-selection inference. Ecology and Evolution 7:5322–5330.

Batary, P., and A. Baldi. 2004. Evidence of an edge effect on avian nesting success. Conservation Biology 18:389–400.

Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile greater sage-grouse in southeastern Idaho. Wildlife Society Bulletin 34:1070–1078.

Blomberg, E. J., J. S. Sedinger, M. T. Atamian, and D. V. Nonne. 2012. Characteristics of climate and landscape disturbance influence the dynamics of greater sage-grouse populations. Ecosphere 3:article 55.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157: 281–300.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

Conover, M. R., J. S. Borgo, R. E. Dritz, J. B. Dinkins, and D. K. Dahlgren. 2010. Greater sage-grouse select nest sites to avoid visual predators but not olfactory predators. Condor 112:331–336.

Eng, R. L. 1955. A method for obtaining sage grouse age and sex ratios from wings. Journal of Wildlife Management 19:267–272.

Gibson, D., E. J. Blomberg, M. T. Atamian, S. P. Espinosa, and J. S. Sedinger. 2018. Effects of power lines on habitat use and demography of greater sage-grouse (*Centrocercus urophasianus*). Wildlife Monographs 200:1–41.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

Giles, E. F., and K. L. Brown. 2015. UDI directory of electric power producers and distributors. 123rd edition of the electrical world directory. Platts, McGraw Hill Financial, New York, New York, USA.

Green, R. H. 1979. Sampling design and statistical methods for environmental biologists. Wiley and Sons, New York, New York, USA.

Hansen, E. P., A. C. Stewart, and S. N. Frey. 2016. Influence of transmission line construction on winter sage-grouse habitat use in southern Utah. Human-Wildlife Interactions 10:169–187.

Homer, C. G., C. L. Aldridge, D. K. Meyer, M. J. Coan, and Z. H. Bowen. 2009. Multiscale sagebrush rangeland habitat modeling in southwest Wyoming. U.S. Geological Survey Open-File Report 2008-1027, Reston, Virginia, USA.

Homer, C. G., C. L. Aldridge, D. K. Meyer, and S. J. Schell. 2012. Multiscale remote sensing sagebrush characterization with regression trees over Wyoming, USA: laying a foundation for monitoring. International Journal of Applied Earth Observation and Geoinformation 14:233–244.

Johnson, D. H., M. J. Holloran, J. W. Connelly, S. E. Hanser, C. L. Amundson, and S. T. Knick. 2011. Influences of environmental and anthropogenic features on greater sage-grouse populations, 1997-2007. Pages 407–450 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitat. Studies in Avian Biology, volume 38. University of California Press, Berkeley, USA.

Kirol, C. P., J. L. Beck, S. V. Huzurbazar, M. J. Holloran, and S. N. Miller. 2015. Identifying greater sage-grouse source and sink habitats for conservation planning in an energy development landscape. Ecological Applications 25:968–990.

Kohl, M. T., T. A. Messmer, B. A. Crabb, M. R. Guttery, D. K. Dahlgren, R. T. Larsen, S. N. Frey, S. Liguori, and R. Baxter. 2019. The effects of electric power lines on the breeding ecology of greater sage-grouse. PLoS ONE 14(1):e0209968.

Kurzejeski, E. W., L. D. Vangilder, and J. B. Lewis. 1987. Survival of wild turkey hens in north Missouri. Journal of Wildlife Management 51:188–193.

LeBeau, C. W., G. D. Johnson, M. J. Holloran, J. L. Beck, R. M. Nielson, M. E. Kauffman, E. J. Rodemaker, and T. L. McDonald. 2017. Greater sage-grouse habitat selection, survival, and wind energy infrastructure. Journal of Wildlife Management 81:690–711.

Liebezeit, J. R., J. Kendall, S. Brown, C. B. Johnson, P. Martin, T. L. McDonald, D. C. Payer, C. L. Rea, B. Streever, A. M. Wildman, and S. Zack. 2009. Influence of human development and predators on nest survival of tundra birds, Arctic Coastal Plain, Alaska. Ecological Applications 19:1628–1644.

Manly, B. F. J. 2006. Randomization, bootstrap and Monte Carlo methods in biology. Third edition. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Manly, B. F. J., L. L. McDonald, and D. Thomas, editors. 1993. Resource selection by animals: statistical design and analysis for field studies. Chapman & Hall, London, United Kingdom.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Springer, Dordrecht, Netherlands.

McDonald, T. L., B. F. J. Manly, R. M. Nielson, and L. V. Diller. 2006. Discrete-choice modeling in wildlife studies exemplified by northern spotted owl nighttime habitat selection. Journal of Wildlife Management 70:375–383.

Naugle, D. E., K. E. Doherty, B. L. Walker, M. J. Holloran, and H. E. Copeland. 2011. Energy development and greater sage-grouse. Pages 489–503 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, volume 38. University of California Press, Berkeley, USA.

Nur, N., A. L. Holmes, and G. R. Geupel. 2004. Use of survival time analysis to analyze nesting success in birds: an example using loggerhead shrikes. Condor 106:457–471.

Qian, S. S., R. S. King, and C. J. Richardson. 2003. Two statistical methods for the detection of environmental thresholds. Ecological Modelling 166:87–97.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in Mark and SAS. Animal Biodiversity and Conservation 27:187–205.

Schroeder, M. A. 2010. Greater sage-grouse and power lines: reasons for concern. Washington Department of Fish and Wildlife, Bridgeport, USA.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus Urophasianus*). Account 425 *in* A. Poole and F. Gill, editors. The birds of North America. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.

Shirk, A. J., M. A. Schroeder, L. A. Robb, and S. A. Cushman. 2015. Empirical validation of landscape resistance models: insights from the greater sage-grouse (*Centrocercus urophasianus*). Landscape Ecology 30:1837–1850.

Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. Journal of Wildlife Management 76:336–347.

Therneau, T. M. 2015. coxme: mixed effects Cox models. R package version 2.2-4. http://CRAN.R-project.org/package¼coxme. Accessed 2 Jul 2018.

Therneau, T. M., B. Atkinson, and B. Ripley. 2019. Rpart: recursive partitioning and regression trees. R package version 4.1-00. http://CRAN.R-project.org/package=rpart. Accessed 2 Jan 2019.

Thomas, D. L., and E. J. Taylor. 2006. Study designs and tests for comparing resource use and availability II. Journal of Wildlife Management 70:324–336.

U.S. Department of Agriculture. 2009. NAIP Imagery-1m (RGBIR)-Wyoming (2009). USDA Farm Service Agency Aerial Photography Field Office, Salt Lake City, Utah, USA.

U.S. Department of Agriculture. 2012. NAIP Imagery-1m (RGBIR)-Wyoming (2012). USDA Farm Service Agency Aerial Photography Field Office, Salt Lake City, Utah, USA.

U.S. Geological Survey. 2015. National Elevation Dataset (NED). Raster digital data. USGS, Sioux Falls, South Dakota, USA. http://nationalmap.gov. Accessed Dec 2014.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

Wallestad, R. O., and D. B. Pyrah. 1974. Movement and nesting of sage grouse hens in central Montana. Journal of Wildlife Management 38:630–633.

Walters, K., K. Kosciuch, and J. Jones. 2014. Can the effect of tall structures on birds be isolated from other aspects of development? Wildlife Society Bulletin 38:250–256.

Westover, M., J. Baxter, R. Baxter, C. Day, R. Jensen, and S. Petersen. 2016. Assessing greater sage-grouse selection of brood-rearing habitat using remotely-sensed imagery: can readily available high-resolution imagery be used to identify brood-rearing habitat across a broad landscape? PLoS ONE 11(5):e0156290.

Wisinki, C. L. 2007. Survival and summer habitat selection of male greater sage-grouse (*Centrocercus urophasianus*) in southwestern Montana. Thesis, Montana State University, Bozeman, USA.

Associate Editor: Timothy Fulbright.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.